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INVASION NOTE

Influence of reproductive state and temperature on the functional response of the marbled crayfish, *Procambarus virginalis*

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Abstract Predictive information on the trophic impacts of an invasive consumer can be gained by experimentally measuring its functional response—the rate of prey consumption in relation to available prey density. However, a common gap in such information is how functional response varies with the consumer's reproductive state and thermal environment. Here, we tested the effect of reproductive state and temperature on the functional response of the marbled crayfish (*Procambarus virginalis*), a parthenogenetic species that is popular in the pet trade and considered to be an invasion threat to freshwater habitats globally, including the North American Great Lakes. We applied two thermal treatments: 18 °C and 26 °C, representing current and projected mean summer surface water temperatures, respectively, for nearshore areas of the lower Great Lakes. We found that gravid individuals readily fed on benthic invertebrate prey (chironomid larvae), but their rate of consumption was substantially reduced compared with non-gravid individuals at both temperatures. When tested at 26 °C, the functional response of gravid individuals did not change, whereas non-gravid individuals exhibited an increase in attack rate and a reduction in maximum feeding rate. A generalized linear model of bootstrapped attack rates and handling times showed that these parameters were affected by temperature and reproductive state. In addition, warming altered reproductive cycles by increasing the frequency and duration of gravid states. Our findings suggest that invasive species risk assessments would be better informed by quantifying variation in invader *per capita* effects across reproductive cycles and temperatures.

Keywords Crayfish · Feeding behaviour · Gravid state · Reproduction · Thermal ecology

Introduction

The impact of a non-native species population is a function of its abundance and *per capita* effects (Dick et al. 2017). Myriad direct and indirect ecological impacts have been linked to the invader's *per capita* rates of resource consumption in ecosystems where such resources (e.g. food, water, habitat space) are limiting (Morrison and Hay 2011; Ricciardi et al. 2013; Dick et al. 2013). High-impact invaders also tend to have higher reproductive rates (Keller et al.

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2007; Ricciardi et al. 2013) and can thus attain abundances that amplify their *per capita* effects on native species (Bradley et al. 2019).

Resource consumption rates can be compared across taxa, populations, locations and environmental conditions (such as temperature), using experimental measurements of an invader's functional response—its rate of resource consumption in relation to resource availability (prey density). Though not without their own challenges (e.g., Griffen 2021), comparisons of functional responses can yield quantitative data on the *per capita* effects of potential or emerging invaders, and thus can inform risk assessments that otherwise must rely upon data from well-studied populations. Two key parameters of the functional response have significance for understanding consumer-resource interactions: attack rate and prey handling time. Higher attack rates increase predation pressure at low prey densities, whereas shorter handling times increase maximum feeding rates (Pritchard et al. 2017). Higher maximum feeding rates have been linked to greater impacts on prey populations in the field (e.g., Dick et al. 2013; Mofu et al. 2019). It should be noted, however, that reduced experimental times and the exclusion of certain complexities of predator–prey interactions (such as reproductive states, prey-switching, and habitat complexity) can lead to overestimates of functional response parameters (Griffen 2021; Choo et al. 2021; Médoc et al. 2018); but they have nevertheless been shown to be useful for predicting and prioritizing the relative risks of invaders under different ecological contexts (Dick et al. 2013).

Procambarus virginalis: an emerging invasive species threat

Among the emerging invasion threats in various aquatic habitats worldwide is the marbled crayfish (*Procambarus virginalis*), also known as 'marmorkrebs', an asexually reproducing species that originated as a novel genotype in the German aquarium trade and gained attention as the only known obligate parthenogenetic crayfish (Lyko 2017). This uncommon reproductive trait is thought to have arisen from a mutation in captive populations of the American Slough crayfish *Procambarus fallax*, making *P. virginalis* a triploid descendant now generally regarded as a distinct species with no defined native range (Vogt et al. 2019; Lyko 2017). Following its increasing commercial availability and numerous unauthorized releases, its invaded range spans parts of Europe, Asia, and Africa (Jones et al. 2009; Faulkes et al. 2012; Chucholl et al. 2012). Given that *P. virginalis* is a fast growing, early maturing and highly fecund species (Seitz et al. 2005), and is the most popular crayfish in the North American pet trade (Faulkes 2015), it is considered an invasion threat to the Great Lakes region (Davidson et al. 2021)—an assessment that is supported by the recent discovery of an established population of marbled crayfish in an urban pond in Ontario, Canada (P. Hamr, *pers. comm.*).

To date, the ecological impacts of *P. virginalis* have been scarcely documented (Lipták et al. 2019). Recent efforts have been made to predict its potential effects and competitive ability in comparison with other crayfishes (Jones et al. 2009; Faulkes et al. 2012; Chucholl and Chucholl 2021; Marn et al. 2022). Yet parthenogenetic reproduction contributes to its impact risk, as ecologically disruptive invaders typically possess traits that confer an ability to attain high population densities (Keller et al. 2007; Ricciardi et al. 2013). For example, individual *P. virginalis* can produce 40% more pleopodal eggs than equal-sized red swamp crayfish (*Procambarus clarkii*), a highly invasive congeneric species (Vogt 2021), although *P. virginalis* grows slower than *P. clarkii* (Kouba et al. 2021). Both its remarkable fecundity and self-cloning ability increase risks of introduction and establishment, as hobbyists' aquaria quickly become overrun, and a single released individual could be sufficient to trigger exponential population growth (Chucholl et al. 2012).

Despite observed variation of feeding rates across reproductive cycles in various crayfishes (Little 1976; Gutiérrez-Yurrita and Montes 1999), comparative feeding rates of gravid versus non-gravid individuals have not been quantified previously. Crayfishes in general have been observed to reduce feeding when females are gravid (Little 1976; Linzmaier and Jeschke 2020), and for this reason egg-bearing females are typically omitted from functional response experiments (Linzmaier and Jeschke 2020). However, for a species with an exceptional reproductive capacity like *P. virginalis*, even small *per capita* effects could be magnified by population growth in a rapidly shifting thermal environment.

Given that reproductive cycles and feeding rates are both mediated by temperature (Seitz et al. 2005), and climate warming is expected to alter trophic interactions in aquatic systems (Veselý et al. 2019; Madzivanzira et al. 2021), we conducted experiments in the laboratory to quantify differences in the functional responses of gravid and non-gravid female crayfish, and thus of reproductive cycles, in response to an increase in temperature. Furthermore, as a parthenogenetic species, *P. virginalis* is a valuable model organism for studying the effect of reproductive state on resource consumption under different thermal regimes. Specifically, we tested the hypotheses that marbled crayfish would exhibit: (1) reduced but non-negligible feeding rates in their gravid state; (2) higher feeding rates at warmer temperatures irrespective of gravid state, owing to greater energetic demands; and (3) an increased number of reproductive cycles at warmer temperatures.

Methods

Animal provenance and care

Procambarus virginalis individuals were obtained from a local pet breeder and housed in temperature-controlled chambers for the duration of our experiments. As crayfish are territorial and aggressive, individuals were kept in their own holding tanks (27.9 × 16.8 × 13.7 cm) supplied with a shelter (a 10-cm segment of PVC pipe) and air stones. Each crayfish was fed two sinking shrimp pellets (Wardley, USA) every two days. Between the months of May to October, the gravid state of each individual was assessed daily. To maintain water quality, 75% water replacement was done at the end of every week (Linzmaier and Jeschke 2020). Crayfish are habitually nocturnal (Larson and Olden 2016), so they were kept on a reversed 12:12 day:night cycle, with lighting provided from 20h00 to 08h00, to ensure peak activity was recorded during experiments.

Crayfish were held at 18 °C for 2 weeks while they acclimated to the laboratory environment. For those individuals that were intended to be used in a high-temperature treatment (26 °C, see below), chamber temperature was increased by 1 °C per day until 26 °C was reached, and then the crayfish were left to acclimate to this higher temperature for 10 days (Whitledge and Rabeni 2002).

Comparative functional response experiments

Experiments were conducted at 18 °C and 26 °C, which represent the current mean and projected mean maximum nearshore surface water temperatures, respectively, for the lower Great Lakes for the period 2070–2100 (Trumpickas et al. 2015). The higher temperature, 26 °C, is within the optimal thermal range of *P. virginalis* growth (25–30 °C; Seitz et al. 2005). Non-gravid crayfish were only used if they had neither molted nor been gravid for at least 1 week prior. Gravid crayfish were tested at any point during egg development until offspring appendages and eyespots became visible, and the egg was no longer easy to delineate (King 1993; Reynolds 2002). To standardize hunger levels, experimental trials were run instead of an individual's scheduled feeding, at which point non-gravid and gravid crayfish were moved from their holding tanks to experimental tanks 1 h prior to experiments (Grimm et al. 2020).

In experimental trials, crayfish were offered bloodworms (*Chironomus* larvae) at one of eight densities (n = 5, 15, 25, 50, 100, 140, 160, and 180) assigned randomly. Bloodworms were kept frozen until needed and then thawed immediately before being introduced to the experimental tanks. Frozen bloodworms allowed for large numbers of easily stored and promptly available prey items of a standard size, which are readily consumed by crayfish (Rosewarne et al. 2016). Although a reduction in handling time can be expected from the use of non-mobile prey, it does not affect functional response comparisons across treatments.

Experiments were run for 3 h in darkness, after which the crayfish were removed from the tank and the remaining prey were counted (South et al. 2019; Linzmaier and Jeschke 2020; Madzivanzira et al. 2021). This procedure was replicated eight times for each prey density within each treatment. Trials were completed in a randomised order. Re-used experimental crayfish were given five days of recovery prior to being used in a new trial (Rosewarne et al. 2016; South et al. 2019). Individuals were never re-used at the same prey density within the same reproductive state.

Statistical analyses

Statistical analyses were conducted using R (version 4.1.2) and the *frair* package (Pritchard et al. 2017). For each treatment, we selected a model using Juliano's method (*frair_test* function of the *frair* package), which tests for evidence of Type II or Type III responses (Pritchard et al. 2017). Note that Type I functional response responses are generally exclusive to filter feeders (Jeschke et al. 2004) and are not relevant to our study.

The selected model was fitted to the data with the *frair_fit* function of the *frair* package, which uses maximum likelihood estimation (Pritchard et al. 2017). As we only found Type II curves, we fitted data with Rogers' random predator equation for non-replaced prey (Alexander et al. 2012; Grimm et al. 2020). From these fitted model equations, attack rate (a) and handling time (h) were extracted.

Fitted functional responses were then compared using three methods. The first method used a z-test (*frair_compare* function of the *frair* package). The second method was a visual comparison of the 95% confidence intervals (CI) of each functional response (created by bootstrapping the fits using the *frair_boot* function of the *frair* package; $n=999$), where CI overlap denotes no statistical difference. The third method relies on bootstrapping the fits 30 times to generate multiple estimates of associated parameters (attack rate and handling time), and modelling these with a generalized linear model using a quasi-Poisson distribution (South et al. 2019). Thus, we modelled both bootstrapped estimates of attack rates and handling times in function of temperature, reproductive state, and their interaction term, then ran a Type III ANOVA and Wald's χ^2 using the *car* package (Fox & Weisberg 2019) to report the effect size of our explanatory variables on our response variables (South et al. 2019).

To measure differences in total days spent gravid and total clutch number, a generalized linear model and a Type II ANOVA with Wald's χ^2 were used to test data collected during daily care assessments. The time spent in gravid condition was measured as the number of days in which crayfish were brooding eggs or young, out of a possible 184 days. Total clutch number was defined as the number of clutches attempted within the recorded time frame. In the generalized linear model, total days spent gravid and total clutch number were the response variables whereas temperature was the explanatory variable. Total days spent gravid per clutch, defined as the number of consecutive days a crayfish spent brooding eggs or young per clutch, was modelled with a generalized linear mixed model using the *nlme* package (Pinheiro et al. 2023) and a Type II ANOVA using Wald's χ^2. As crayfish could have multiple clutches within the given time frame, we modelled days spent gravid per clutch in relation to a fixed effect of temperature and individual crayfish ID as a random effect.

Results

Functional response type did not change with reproductive state or temperature treatment; all curves fitted in this experiment were Type II responses (Fig. 1). Overall, maximum feeding rates of non-gravid individuals were reduced at 26 °C compared with 18 °C (Fig. 1). Gravid individuals consumed substantially less prey than non-gravid individuals at both temperatures (Fig. 1; Table 1). Our results also indicated that, when gravid, *P. virginalis* attack rates decline and handling times increase (Tables 1 and 2). This finding was further informed by our generalized linear model results, which showed a strong significant influence of reproductive state and of temperature on both attack rates and handling times (Table 3; both $p<0.05$). Reproductive state also had an interactive effect with temperature on both attack rate and handling time (Table 3; both $p<0.001$). The maximum feeding rate of gravid compared to non-gravid individuals was reduced by 93% at 18 °C and by 85% at 26 °C (Fig. 1).

The total number of days (from May to October) that individuals spent in the gravid state did not differ with temperature (GLM: $\chi^2=0.55$; $p=0.46$). However, individuals at 26 °C spent significantly less time gravid per clutch and had significantly more clutches than individuals at 18 °C (GLMM: $\chi^2=75.79$; $p<2.2\times10^{-16}$, and GLM: $\chi^2=14.97$; $p=0.00011$, respectively).

Discussion

Effects of reproductive state on feeding behaviour

Our results revealed the extent to which gravidness affects the functional response of *P. virginalis*

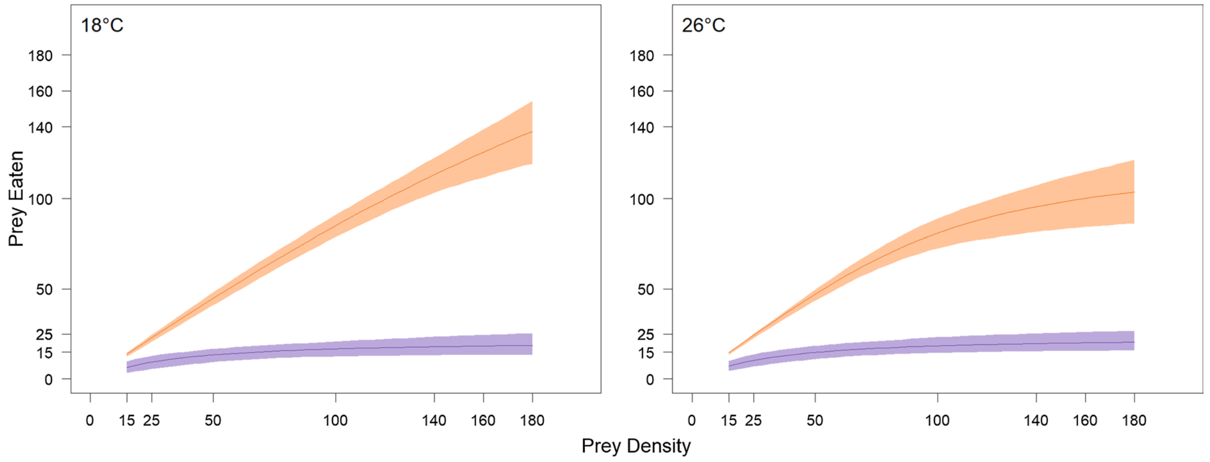

Fig. 1 Functional responses with bootstrapped 95% confidence intervals (n = 999) for gravid (purple) and non-gravid (orange) *P. virginalis* at 18 °C and 26 °C. Lines represent the best fit model for each population (Type II)

Table 1 Fitted coefficients for each gravid and non-gravid functional responses at both temperatures

Treatment	Type	First-order	*a*	*h*	1/*h*
Gravid 18 °C	II	−0.0098***	0.28***	0.14***	7.19
Normal 18 °C	II	−0.0082***	0.89***	0.010***	100
Gravid 26 °C	II	−0.012***	0.32***	0.13***	7.81
Normal 26 °C	II	−0.017***	1.50***	0.023***	43

Asterisks denote significant *p* values (*** < 0.001)

at different temperatures. Reduced feeding during gravid stages has previously been shown for multiple crayfish species to occur shortly after the female has deposited her eggs and continues through a feedback loop of brooding pheromones until the larvae disperse (Little 1976; Reynolds 2002). During this time, female metabolism slows down (Gutiérrez-Yurrita and Montes 1999), and reduced feeding behaviour is observed (Little 1976). However, to our knowledge, differences in crayfish functional response during critical life history stages have not been previously quantified.

Though the maximum feeding rates of gravid individuals in our experiment were significantly higher than zero, functional response experiments to date have tested only male or non-gravid female crayfish (Linzmaier and Jeschke 2020; Chucholl and Chucholl 2021). Given the capacity for every individual within a population of *P. virginalis* to become gravid at some point during its lifespan, changes to the functional response induced by this state should be explicitly considered in impact metrics (Dick et al. 2017; Dickey et al. 2018). Where such information is lacking, *per capita* effects—and ultimately field impacts—could be underestimated when population densities are high. For example, based on the observed differences in the maximum feeding rates of

Table 2 Results of z-tests of the attack rates (*a*) and handling time (*h*) between the fitted gravid and non-gravid functional responses at both temperatures

Fit 1	Fit 2	Parameter	Estimate	Std. Error	*p*-value
Gravid 18 °C	Gravid 26 °C	Δa	−0.04	0.055	0.46
		Δh	0.01	0.011	0.28
Normal 18 °C	Gravid 18 °C	Δa	0.61	0.059	< 0.001***
		Δh	−0.12	0.0085	< 0.001***
Normal 26 °C	Gravid 26 °C	Δa	1.19	0.01	< 0.001***
		Δh	−0.1	0.0068	< 0.001***
Normal 18 °C	Normal 26 °C	Δa	−0.62	0.10	< 0.001 ***
		Δh	−0.013	0.001	< 0.001***

Asterisks denote significant *p* values (*** < 0.001)

Table 3 Results from GLM with a quasi-Poisson error distribution used to determine differences in bootstrapped estimates of attack rate and handling times with regards to reproductive state and temperature, using a Type 3 ANOVA and Wald's χ^2 to report the effect size of our explanatory variables on the response variable

Factor	Chi-square	Df	*p*-value
(a) Attack rates			
Reproductive state	223.13	1	$<2.2\times10^{-16}$***
Temperature	8.52	1	0.0035**
Reproductive state × temperature	13.26	1	0.00027***
(b) Handling times			
Reproductive state	1722.91	1	$<2.2\times10^{-16}$***
Temperature	33.94	1	5.69×10^{-9}***
Reproductive state × temperature	64.79	1	8.33×10^{-16}***

Asterisks denote significant *p* values (**$p<0.0$; ***$p<0.001$)

gravid versus non-gravid females in our experiment, we estimate that the feeding rate of a non-gravid individual is matched by 5.5 gravid individuals at 18 °C, and by 13.9 gravid individuals at 26 °C.

Effects of temperature

Although the higher temperature treatment in our study is within the reported range of temperatures at which growth *P. virginalis* in the laboratory is maximal (i.e., 25–30 °C; Seitz et al. 2005), and functional responses are hypothesized to be higher at temperatures approaching the thermal growth optimum of the consumer (Iacarella et al. 2015), maximum feeding rates of non-gravid individuals were reduced at 26 °C compared with 18 °C (Fig. 1).

For *P. virginalis* and other species whose invasion risk have been linked to parthenogenesis, we speculate there could be a trade-off between two key traits of invasion success: reproductive ability and the exploitation of resources necessary to sustain an incipient population. A similar balance exists between somatic growth and resource consumption, particularly in individuals whose feeding is also reduced by molting during ecdysis (Reynolds 2002). At least for *P. virginalis* in the laboratory, the effect of temperature on consumption is more important through its interactive effects with reproduction, especially as warmer temperatures typically provoke higher energetic demands (Carreira et al. 2017).

From May to October, individuals in our laboratory population spent the same total number of days in a gravid state at both temperatures. Warmer temperatures accelerated hatch time, whereby individuals at 26 °C spent less time gravid per clutch, but this may also be linked to a lower larval survival rate (King 1993; Aydın and Dilek 2004). However, the number of clutches also increased with temperature; individuals had more clutches at 26 °C than at 18 °C, which could potentially balance against the mortality caused by shorter hatch times such that exposure to the warmer temperature would cause no overall reduction of fecundity. It is worth noting that our experiments tested a cultivated population kept at both 18 °C and 26 °C for longer periods than they would experience under seasonal variation in the wild. For this reason, the frequency of reproductive events in our laboratory population could differ from wild populations, which have thus far been observed to spawn 1–3 times per year (Vogt et al. 2019; Vogt 2021).

Importance for management

These findings and those of a recent study (Dalal et al. 2021) underscore the value of comparing *per capita* effects across phenological and ontogenetic stages of invasive animals to better inform risk assessment. In a study comparing functional responses of female *Gammarus pulex* amphipods that were either non-ovigerous or had embryonic broods, Dalal et al (2021) found that females carrying immature-stage embryonic broods had significantly higher attack rates than those with mature-stage embryonic broods. Thus, functional response experiments that account for changes in the reproductive cycle of a consumer can reveal more nuanced information concerning their trophic interactions.

Our observations show that changing temperature contexts affect not only the consumption rate of *P. virginalis* but also their reproductive cycles. Quantifying these responses under different environmental conditions allows us to better characterize variation in *per capita* effects as well as the potential impact of an established population under climate warming (Iacarella et al. 2015; Dickey et al. 2018), though these experiments might not predict the entire range of their thermal responses in the wild (cf. Marshall et al. 2021). In the present study, we tested aquarium-reared individuals of *P. virginalis* because the species is most likely to invade the Great Lakes region and other inland water bodies through pet release. We recommend that similar tests be done on self-sustaining *P. virginalis* populations in the wild. Ultimately, knowledge of climatic and other environmental influences on crayfish reproductive state and behaviour can inform invasive species management practices (see Gutiérrez-Yurrita and Montes 1999).

Author contributions NS and AR contributed to the study conception and design. Data collection was performed by NS and JP. Data analysis was conducted by NS. The manuscript was written by NS, and all authors contributed to subsequent editing and have approved the final manuscript.

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Data availability Experimental data will be made available in Dryad.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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